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Habitat Associations of Wetland Butterflies Near the Glacial Maxima in Ohio, Indiana, and Michigan

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Abstract. Thirty-seven wetland complexes were analyzed and the habitat associations of 15 wetland butterfly species were determined. Species which are restricted to specific wetland types include *Oarisma poweshiek, Euphyes bimacula, Epidemia dorcas, Calephelis muticum, Neonympha mitchellii* (all bog fens), *Euphyes dukesi* (swamps), and *Charidryas harrisii* (sedge meadow). Species which are less restrictive in habits are *Poanes massasoit* (bog and prairie fens), *Poanes viator* (sedge meadows, bog fens, and swamps), *Euphyes dion* (sedge meadows and bog fens), *Euphyes conspicua* (sedge meadows, bog fens, and bogs), *Hyllolycaena hyllus* (marshes, sedge meadows, bog fens, prairie fens, and bogs), *Euphydryas phaeton* (sedge meadows, bog fens, and prairie fens), *Satyrodes eurydice* (sedge meadows, bog fens, prairie fens, and bogs), and *Satyrodes appalachia* (bog fens and swamps). Fens contain the most diverse butterfly assemblages of the wetland types considered. Only two species, *E. phaeton* and *H. hyllus,* occur in the poorly developed wetlands south of the glacial maxima.

Three ecologically segregated pairs of closely related species occur in the study areas (*S. eurydice-S. appalachia, E. dion-E. dukesi,* and *P. viator-P. massasoit*). These species pairs often coexist in the same wetland complexes but seldom interact due to differing habitat requirements.

Introduction

Wetland biological communities contain many of the rarest and most interesting plant and animal species native to the Great Lakes Region. Many plant species are restricted to these habitats because of strict soil or micro-habitat requirements, or because of reduced competition from weedy species within these habitats. These plants are often parasitized by insects which, like many parasites, are host specific and are thus also limited to wetlands.

Five basic types of wetland communities occur in Ohio, northeastern Indiana and southeastern Michigan (Curtis, 1959; Pringle, 1980). They are generally characterized as pioneer, now often relict communities that occur in isolated pockets of poor drainage and cool microclimate. Open wetlands represent communities which may have been characteristic of

plant associations adjacent to the retreating glacier. Wooded wetlands represent communities which replaced the pioneering communities as a result of natural habitat modifications. In addition to floristic differences, the community types generally differ in drainage patterns, soil types, and soil pH. The following descriptions describe those elements which are characteristic and therefore aid in the recognition of the various wetland types in their purest states. Many areas however, are mosiacs of wetland types and transitional communities are frequently encountered.

Marshes are the wettest of the habitats with water above the soil during much or all of the growing season. They often develop along streams and lake shores. The soil usually contains a high mineral content, even in areas where it superficially resembles organic muck. Typical plants are mostly herbaceous and include cattail (*Typha latifolia* L.), bulrush (*Scirpus validus* Vahl.), and occasionally blueflag (*Iris versicolor* L.).

Sedge meadows are similar to marshes and occur in the same situations, but are only seasonally flooded. The soils are usually sedge peat or organic muck. These wetlands are open communities dominated by sedges (*Carex spp.*) with scattered horsetails (*Equisetum spp.*), blueflag, and cattails.

Fens occur in depressions with impeded drainage in areas of calcareous substrates. They are generally found along streams or lake shores and are usually fed by springs. The soils are sedge peat and are neutral to highly alkaline. Two types of fens occur in the study area which differ primarily in the relict plant species present (Stuckey & Denny, 1981). **Bog fens** contain many plants of northern distributions such as pitcher-plant (*Sarracenia purpurea* L.), tamarack (*Larix laricina* [Du Roi]) and poison sumac (*Rhus vernax* L.). **Prairie fens** contain a significant number of prairie species, the most conspicuous of which is big blue-stem (*Andropogon gerardi* Vitman). Both types of fens contain extensive stands of sedges and shrubby cinquefoil (*Potentilla fruticosa* L.), and often contain lady slippers (*Cypripedium spp.*). Fens or parts thereof which are dominated by shrubs such as red-osier (*Cornus stolonifera* Michx) and willows (*Salix spp.*) are referred to as **carrs. Treed fens** are dominated by trees suich as tamarack, white cedar (*Thuja occidentalis* L.), or maples (*Acer spp.*). Because fens superficially resemble bogs, most named fens often contain the term.

Bogs are found in depressions, usually glacial kettle holes with completely impeded drainage. Bogs are fed by rain and ground water and there is often a remnant of open water in the center. The soil is sphagnum peat and is highly acidic. Bogs are dominated by mosses of the genus *Sphagnum* which form an almost complete ground cover usually obscured by taller plants. Ericaceous shrubs such as blueberries and cranberries (*Vaccinium spp.*) and leatherleaf (*Chamaedaphne calyculata* [L.]) form a conspicuous element in these habitats. Other distinctive plants include pitcherplant, cottongrasses (*Eriophorum spp.*), sundews

(*Drosera spp.*) and several orchids. **Wooded bogs** are dominated by tamarack with scattered poison sumac.

Swamps occur along streams and rivers and are seasonally or permanently flooded. Swamp soils are high in organic matter but are not peaty. They are dominated by trees such as willows, maples, buttonbush (*Cephalanthus occidentalis* L.), and red-osier. Herbaceous plants include various sedges and skunk cabbage (*Symplocarpus foetidus* [L.]).

The wetlands of the study area support 15 species of butterflies not typically encountered in other habitats. These butterflies and their hostplants must have invaded the region after the Wisconsin glaciation from refugia located somewhere south of the glacial boundary as habitats became available (about 15,000 B.P.). An east-west route may have existed from the Atlantic Coastal Plain to the Great Lakes region via the once flooded Mohawk Valley in New York (Peattie, 1922; Shapiro, 1970). Species which may have followed this route are *Neonympha mitchellii* French and *Euphyes bimacula* (Grote and Robinson). Alternately, the Mississippi Valley may have allowed invasion of the Great Lakes region from refugia located on the Gulf Coastal Plain. Probable butterfly examples include *Satyrodes eurydice* (Johansson) and *Calephelis muticum* McAlpine. Pollen profiles from several Great Lake Region sites indicate that this migration took place between 13,000 and 5,000 B.P. in the study area (Vesper and Stuckey, 1977). During the xerothermic period (about 5,000 B.P.), wetlands in these corridors may have been altered resulting in the extinction of many or all of the connecting populations between the refugia and the Great Lakes (Shapiro, 1970).

Materials and Methods

I sampled a total of 24 wetland complexes during the summers of 1982-1984 (Fig. 1, Table 1). The sites were chosen to be representative of the wetland types present throughout the study area. However, undisturbed areas were given priority over disrupted wetlands. Each wetland was sampled at least three times at two week intervals from late June through July to insure that the flight periods of all the wetland species were covered. All available habitats at each site were sampled as thoroughly as possible on each visit. Extensive field notes were taken concerning the habitats of each butterfly species encountered at every site.

Data from a few sites from within the study area are available in the literature and were incorporated unchanged (Albrecht, 1974; McAlpine *et al.*, 1960) or as a supplement to my own sampling (Badger, 1958; Price, 1970; Price & Shull, 1969; Palister, 1927). Specimens in the Ohio State University Museum and the Ohio Historical Society Collection were also examined and specimens with specific locality data were utilized to supplement my sampling. Additional data were solicited from several other collectors as noted in Table 1.

Sedges were identified with the keys in Braun (1967). However, the vast majority of the sedges were not in bloom and were thus not identifiable to species and were categorized simply as broad-leaved or narrow-leaved.

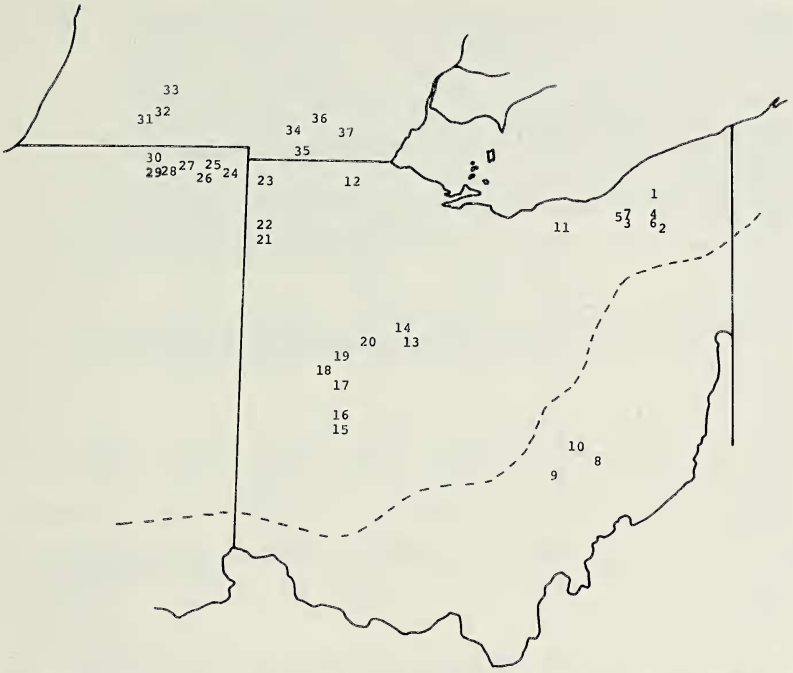

Fig. 1. Approximate locations of wetland complexes analyzed. Dashed line is the Wisconsin glacial maxima. Numbers refer to site numbers in Table 1.

Habitat utilization by *Poanes massasoit* (Scudder) and *P. viator* (Edwards) was determined at Mud Lake in 1983. The fen was divided into seven sections which reflect the limits of mat types as defined by Brodberg (1976) (Figure 2). The distribution of the two species within the fen was determined by walking the perimeter and recording the location of each specimen sighted. The south-west quarter of the fen was not censused because of the fragility of the mat. Seven censuses were taken in July 19-24 between 1000 hrs and 1700 hrs (eastern standard time). Allowing that some individuals may have been recorded more than once per census, a 2x2 contingency table was utilized to analyze this data.

Results

Table 1 lists the sites included and records the different habitats present at each site. All but three of these sites are located in glaciated areas (Figure 1). Over half of the sites are fens which reflects the prevalence of this type wetland throughout the study area. Bogs are absent over the western portion of the study area and are represented by three sites in northeastern Ohio. Nine sites are primarily swamps. Marshes and sedge meadows usually occur in association with other wetland types and were sampled in conjunction with the other sites. Many of the sites are briefly

Site No.	Site Name	Site Description	Marsh	Sedge Meadow	Bog Fen	Prairie Fen	Carr	Treed Fen	Bog	Wooded Bog	Swamp	O. poweshiek	P. massasoit	P. viator	E. dion	E. dukesi	E. conspicua	E. bimacula	H. hyllus	E. dorcas	C. muticum	C. harrisii	E. phaeton	S. eurydice	S. appalachia	N. mitchellii
1	Fern Lake	1						*	x														x			
2	Triangle Lake	1						*	x									x					x			
3	Kent Bog							x	*							x										
4	Eagle Creek	1								*														x		
5	Herrick Preserve	1	x		*		x											x			x		x			
6	Mantua			*									x		x						x	x	x			
7	Gott Fen	1	x	*	x		x						x		x		x	x				x	x			x
8	The Plains			*														x				x				
9	Crane Hollow	1		*						x								x				x				
10	Rockbridge Bog	1		*						x								x				x				
11	Findley State Pk.[a]									*					x									x		
12	Campbell Preserve			x						*			x	x	x	x	x						x	x		
13	Marysville[b]			x						*					x	x								x		
14	Broadway[b]			x						*					x	x								x		
15	Redmond Fen	2				*							x									x	x			
16	Prairie Road Fen	2		x		*							x									x	x			
17	Cedar Bog[c]	1		x	*	x		x					x		x					x		x	x			
18	Liberty Fen					*							x					x				x	x			
19	Urbana Raised Bog	2		x		*							x					x					x			
20	Reams Woods	1		x						*					x	x								x		
21	Junction[d]			x						*					x	x								x		
22	Paulding[d]									*						x								x		
23	Mud Lake[e]	1			*		x						x	x	x		x	x	x				x	x		
24	Cemetary Lake		x	*	x			x					x	x				x				x	x	x		
25	Marsh Lake	3	x	x	*			x		x			x	x	x	x	x			x		x	x	x	x	x
26	Binkley Bog				*			x											x							
27	Beaver Dam Lake	3		x	*								x									x	x			
28	East Mongo	3						*																x		
29	Nasby Fen				*		x												x				x			
30	Cedar Lake[dh]				*		x	x					x	x			x	x		x		x	x	x	x	x
31	Wakelee Bog[dh]			x	*		x	x					x	x	x		x			x		x	x	x	x	x
32	Three Rivers Res.[dh]			x	*		x	x					x		x		x					x	x			x
33	Yankee Springs[d]				*		x	x					x				x		x			x	x			x
34	Liberty Bog			x	*		x	x				x	x	x	x		x		x	x		x	x	x	x	x
35	Morenci[d]									*			x			x								x		
36	Sharon Hollow[g]			x	*								x	x			x	x				x	x			x
37	Milan[d]			x						*			x	x	x	x	x						x			

Table 1. Description of and wetland butterflies recorded from the wetland sites discussed. Site numbers refer to Figure 1. More detailed site descriptions are contained in: 1 - Herrick, 1974; 2 - Cusick and Troutman, 1978; and 3 - Lindsey, *et al.*, 1969. * - denotes the dominant habitat type at each wetland. x - denotes the presence of a habitat type or butterfly species at each wetland. Data from, supplemented from, or courtesy of: a. - L. Martin; b. - J. Calhoun; c. - Albrecht, 1974; d. - M. Neilsen; e. - Price, 1970; f. - Price and Shull, 1969; g. - McAlpine *et al.*, 1960; and h. - Badger, 1958.

Table 2. Wetland butterflies and their habitat associations as recorded in this study. See text for explanation of habitat types.

Species	Marsh	Sedge Meadow	Bog Fen	Prairie Fen	Carr	Treed Fen	Bog	Wooded Bog	Swamp
O. poweshiek			X		X				
P. massasoit		X	X	X					
P. viator		X	X			X			X
E. dion		X	X						
E. dukesi									X
E. conspicua		X	X		X		X		
E. bimacula			X						
H. hyllus	X	X	X	X	X		X		
E. dorcas			X		X				
C. muticum			X						
C. harrisii		X							
E. phaeton		X	X	X					
S. eurydice	X	X	X				X		
S. appalachia						X			X
N. mitchellii			X		X				

described in Herrick (1974), Cusick & Troutman (1978), and Lindsey *et al.* (1969) (Table 1).

Table 1 records the butterflies known from each wetland. *E. bimacula* was not recorded during my sampling, but the species is known from four sites included in this study. Two other species, *Oarisma poweshiek* (Parker) and *Charidryas harrisii* (Scudder) were recorded from only one site each. The remaining species were encountered with regularity in the appropriate habitats.

Table 2 summarizes the habitat associations of each species. Additional comments for three of the species are as follows:

Oarisma poweshiek — Although Opler (1984) records the habitat of this species as "native tall-grass prairie", McAlpine's (1972 [73]) and my observations indicate that it is closely associated with bog fen meadows or carrs in Michigan.

Poanes viator — Shading does not seem to be a factor in the micro-

distribution of *viator*, which is the only species which apparently breeds in both sunny and shady habitats.

Euphyes dukesi (Lindsey) — This species is strictly confined to swamps. At Marsh Lake (primarily a fen) it is restricted to a small swamp even though the presumed hostplant ranges abundantly into the adjacent treed fen.

Figure 2 summarizes the distributions of *Poanes massasoit* and *P. viator* at Mud Lake. A 2x2 contingency table for statistical independence is highly significant (Chi-square = 20.94, $p < 0.005$). Although this test is not entirely appropriate, the high significance indicates the high degree of disassociation between these species.

Discussion

Although the term fen is in general botanical usage, I have never encountered it in reference to North American butterfly habitats even though most references to bogs actually refer to fens (e.g. Albrecht, 1974; McAlpine, *et al.*, 1960; Price, 1970; Price & Shull, 1969; Badger, 1958). Fens in fact support the most diverse butterfly assemblages of the wetland types discussed. The resulting confusion has obscured many important relationships.

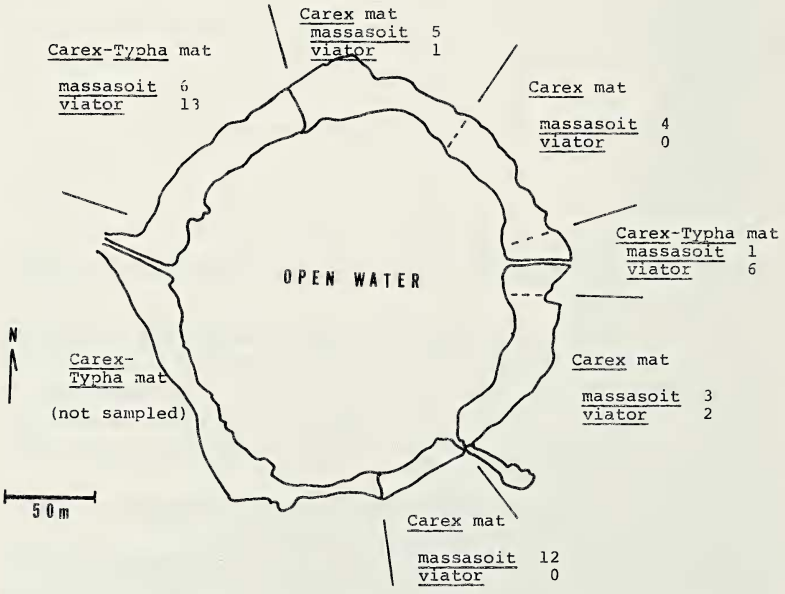

Fig. 2. The distribution of *Poanes massasoit* and *P. viator* at Mud Lake relative to the *Carex* and *Carex-Typha* mats. (Modified from Brodberg, 1976).

Once the habitat associations of each butterfly are known, patchy distributions are better understood and tend to reflect the distribution of certain habitat types. For example, only two wetland species, *Euphydryas phaeton* (Drury) and *Hyllolycaena hyllus* (Cramer), occur south of the glacial maxima where only swamps and poorly developed sedge meadows occur. More subtly, the known distribution of *P. massasoit* in Ohio coincides with the distribution of fens in the western part of the state. Additional sampling will probably locate this species in more of the western Ohio fen areas. However, not all aspects of wetland butterfly distributions are satisfactorally explained by the distribution of differing habitat types. *P. massasoit* is not present in the eastern part of the study area despite the presence of seemingly suitable habitats there.

Four other butterflies are present only in the western study sites, possibly the result of their past biogeographic histories. *E. dukesi* and *C. muticum* are both distributed along the Mississippi Valley (Opler, 1984) and may have migrated from this area into the Great Lakes Region via the valley and its tributaries after the last glaciation. *O. poweshiek* and *Epidemia dorcas* (Kirby) are distributed to the west of the study area and may have migrated eastward along the glacial front as habitats became available from their refugia. Thus, the absence of these species from certain regions may indicate the lack of suitable habitats during the periods of range expansion.

Several related pairs of ecologically segregated species occur in wetlands. These species pairs are usually more closely related to each other than to any other species in the study area. The evidence indicates partitioning of larval resources within the pairs but not with other species or between the species pairs. Shapiro and Carde (1970) reported that *S. eurydice* and *Satyrodes appalachia* (Chermock) segregate on the basis of open versus wooded habitats, a finding supported by this study. Although at certain localities where both species occur, they may utilize the same hostplant species which is effectively partitioned between them. *Eurydice* uses the hostplant in sunny areas and *appalachia* uses the hostplant in shaded areas.

Three other pairs of wetland butterflies also show similar segregation.

Euphyes dion (Edwards) — *E. dukesi*. These species segregate much as do *eurydice* and *appalachia*. Both species are usually associated with *Carex lacustris*, but *dion* occurs in open areas while *dukesi* occurs in shaded habitats. Only once have I observed *dion* inside a swamp feeding on buttonbush. At Marsh Lake, males of both species have been observed feeding in a hay field which ajoins the wetland complex, but within the wetland itself these species do not mix. Of the remaining wetland *Euphyes spp.* in the study area *Euphyes conspicua* (Edwards) is capable of utilizing several *Carex spp.* in open situations, while the hostplant and habitat associations of *E. bimacula* are not well known.

Poanes viator — P. massasoit. Although populations of these species often coexist in sedge meadows, they usually occur in close association with their respective presumed hostplants, *Carex stricta* Lamborn and *C. lacustris*. Both hostplants often form dense stands which superficially resemble monocultures with which the butterflies are intimately associated. I surveyed Mud Lake to identify the principal areas of activity for these two species. In this fen *Carex aquatilis* Wahlenb., a narrow leaved species, dominates the *Carex* mat and occurs less frequently in the *Carex-Typha* mat. *Massasoit* occurs throughout the fen but was most frequently found on the *Carex* mat while *viator* is more restricted and occurs on the *Carex-Typha* mat (Figure 2). At Marsh Lake, where both hostplants form monoculture like stands, the separation of these species is virtually complete although they are often seen at the same nectar sources.

Epidemia dorcas — E. epixanthe (Boisduval and Le Conte). These species segregate by both hostplant and by habitat. *E. epixanthe* was not encountered during this study: its hostplant, large cranberry (*Vaccinium macrocarpon* Ait.), is restricted to highly acidic peat deposits and only forms dense stands in bogs. In fens, *V. macrocarpon* often occurs in older more acidic parts of the mat or in sphagnum hummocks at the base of shrubs, but only as dispersed plants and never in dense stands. *L. dorcas* utilizes shrubby cinquefoil which is limited to alkaline peat deposits (i.e. fens). Thus, populations of these two butterflies would not be expected to interact at any given locale.

How these species pairs formed within the wetlands of eastern North America is an interesting question. Because ecological disassociations found in this study are uniformly restricted to closely related species, the disassociations may represent ecological isolating mechanisms. This appears to be the case in the examples cited of wetland *Satyrodes, Euphyes,* and *Poanes*, which showed no evidence of interspecific courting/mating during this study. Other factors may have helped shape these species pairs. Although no direct evidence exists to support such conjecture, it is interesting to speculate that some process such as interspecific competition for hostplants (Shapiro & Carde, 1970) or divergence of isolated populations within the limited confines of a few wetlands has resulted in the formation of such species pairs. (See Shapiro, 1970). Genetic exchange between many of the populations in this study must be minimal to non-existent due to the vast expanses of unsuitable habitat separating them, but it is unknown how freely populations mixed before humankind altered the landscape or during the previous interglacials. It must be assumed that all of these species possess some dispersal capabilities or they would not occur within glaciated territory.

No doubt the repeated destruction and reformation of wetland habitats during glacial cycles has had a profound effect upon these communities.

Each advance of the ice sheet presumably fragmented and relocated populations of each of these butterflies, possibly to small refugia where certain populations may have been more susceptible to environmentally induced genetic changes. Additionally, each wetland itself slowly undergoes natural succession. These changes (e.g. fens becoming acidic or marshes, fens and bogs becoming wooded) may be gradual enough to allow the subtle ecological differences observed between some of the closely related species to evolve.

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